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STUDIES ON THE PLANT CELL.—IV.

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SECTION III. HIGHLY SPECIALIZED PLANT CELLS AND THEIR PECULIARITIES (*Continued*).

4. The Spore Mother-cell.

THE spore mother-cell and its homologues the pollen mother-cell and certain embryo-sacs have furnished some of the most interesting subjects for cell studies in the plant kingdom. Sporogenesis in all plants above the thallophytes seems to be a period when nuclear structures are especially clearly differentiated and when the mechanism of mitosis reaches the highest degree of complexity. These intricate conditions are only equalled by processes in the development of the female gametophyte of some angiosperms, and during endosperm formation, also in the events of spermatogenesis and with the segmentation of the egg nucleus of certain gymnosperms.

Sporogenesis is one of the critical periods in the life history of a higher plant since it is the time when the asexual generation (sporophyte) passes over to the sexual (gametophyte). This provides certain important features such as the reduction phenomena concerned with chromosomes and greatly adds to the interest in these cells. These matters will receive special attention in Section V, but they must be borne in mind to appreciate fully the significance of many events of spore formation.

The general history of the spore mother-cell may be described as follows: It is the product of the last mitosis in the reproductive tissue called the archesporium. This mitosis always presents the number of chromosomes characteristic of the sporophyte which is double the number found in the gametophyte. Therefore the nucleus that passes into the spore mother-cell has the sporophyte number of chromosomes. Two mitoses occur successively in the spore mother-cell in all forms. The first mitosis presents half the number of chromosomes found in the last nuclear division in the archesporium and is consequently the reduced or gametophyte number. The reduction of the chromosomes then takes place during the period of rest between the last mitosis in the archesporium and the first in the spore mother-cell. There are two mitoses in the spore mother-cell. In some forms these are exactly alike and present essentially the same characters as the usual typical mitoses of plants. But among the spermatophytes there are likely to be peculiarities in the arrangement and distribution of the chromosomes. In consequence the first mitosis may be heterotypic and the second homotypic in contrast to the normal typical conditions. The description and explanation of these characters will be reserved for the groups that illustrate them the best. They have nothing to do with qualitative reduction phenomena as was formerly supposed.

There is sometimes a well defined period of rest after the first mitosis with the formation of a wall between the two daughter nuclei, but frequently the second mitosis follows immediately after the first so that the spore mother-cell comes to contain four daughter nuclei. Cell walls may then be formed between these nuclei simultaneously so that the resultant spores are disposed in a radially symmetrical arrangement that is termed tripartite. These cell divisions are almost universally present in the spore mother-cell, the only exceptions being certain spermatophytes whose megaspore mother-cells develop directly into embryo sacs, the two mitoses (heterotypic and homotypic) being included within these structures and forming a part of the gametophyte history. Why the number of spores should generally be four is unexplained. There does not seem to be any physiological significance in the number or other reasons why it should not be more or less. Indeed it is somewhat variable in the spermatophytes for microspore or pollen mother-cells form two and three pollen grains in certain types and five, six and seven have been found in others, while much larger numbers have been occasionally reported. In no case is the microspore mother-cell known to develop directly into a pollen grain, although the megaspore mother-cell regularly becomes an embryo sac in some forms (*e. g.*, Lilium). But an increasing number of observations indicate that the megaspore mother-cell generally develops two, three or four potential megaspores although normally only one of these becomes an embryo sac.

The interest in the protoplasmic activities of sporogenesis lie chiefly in the elaborate methods of spindle formation and mechanism of mitosis, in the organization and distribution of the chromosomes, in the functions and activities of the nucleolus, and in the organization of the cell plate and development of the cell wall. There is a very extensive literature on the spore mother-cell some of which, however, merely treats the broad features noted in studies of a general morphological character on the development of sporophylls or floral structures. We shall only attempt to consider the most important contributions, and for convenience will begin our treatment with the Hepaticæ and conclude with the spermatophytes where the conditions are the most complex.

The Hepaticæ or liverworts furnish some remarkable spore mother-cells, and are now the subject of considerable interest and some discussion. They were first brought conspicuously to the attention of botanists by a paper of Farmer ('94) on *Pallavicinia decipiens*. Farmer described a remarkable series of events in this type. The nucleus of the spore mother-cell became surrounded before division by dense protoplasm that extended into the four lobes of the cell in the form of a four-rayed star which he called a "quadripolar spindle." After its development four chromatic droplets appeared in the nucleus to indicate its approaching division. These chromatic droplets became four chromosomes which by division were doubled in number. The eight rod shaped chromosomes moved in pairs towards the four lobes of the spore mother-cell. There was a further division of each chromosome, making sixteen in all, and the four groups of four each passed simultaneously to the poles of the "quadripolar spindle" which persisted to the end. It should be noted that the striking peculiarities of Farmer's account lie in the division of the four primary chromosomes into sixteen, and in their simultaneous distribution through a "quadripolar spindle" to form at once four daughter nuclei. These events are unparalleled, as far as the writer is aware, in the plant or animal kingdom, and consequently the account deserves especial attention. A four-rayed figure around the nucleus is not surprising because the spore mother-cell of the Jungermanniales is four lobed, and its centrally placed nucleus lies in a restricted area. But the simultaneous distribution of quadrupled chromosomes to form four daughter nuclei is a process whose establishment would be of fundamental significance. Farmer also described a centrosome at each pole of the "quadripolar spindle."

Farmer ('95*a*, *b*, and *c*) followed his paper on Pallavicinia with studies on other liverworts. He reported the "quadripolar spindle" in the early stages of mitosis in several of the Jungermanniales, but did not find the quadrupling and simultaneous distribution of the chromosomes as in Pallavicinia. The "quadripolar spindle" when present was a temporary structure replaced later by the bipolar spindles of two successive mitoses with a longer or shorter interval between. Farmer considers the "quadripolar spindle" of these forms as transitional between that of Pallavicinia and the normal bipolar spindle. The Ricciales, Marchantiales and Anthocerotales present two successive mitoses after the usual manner in the spore mother-cell.

The writer has described the events of sporogenesis in Pellia (one of the Jungermanniales) in a paper covering the nuclear activities at several periods in its life history (Davis, :01), and confirmed much of Farmer's account of the mitoses in this spore mother-cell. These are two in number and successive, with a very well defined resting period between the first and the second. There is a four-rayed figure present during the prophase of the first mitosis, and this seems to correspond to Farmer's "quadripolar spindle." The nucleus lying in the center of the four lobed spore mother-cell becomes invested by a kinoplasmic sheath which develops a fibrillar structure. Many of these fibrillae extend into the lobes of the spore mother-cell because the nucleus is confined to a narrow space in the constricted central region of the cell and the lobes offer the only possible relief for the crowded conditions. However, the four-rayed structure is not present when the chromosomes are ready for distribution, but there is found instead one large, broad poled spindle. (See Fig. 5 *c*.) A cell wall is formed between the two daughter nuclei (Fig. 8 *d*) which divide again after a very short period of rest, the two spindles lying at right angles to one another. The poles of the spindles are rather blunt, and there are no centrosomes or centrospheres in either mitosis. The four-rayed structure of prophase must be regarded as preliminary to spindle formation because the chromosomes are not ready for distribution, and when that period arrives the structure has been replaced by the true spindle of the first mitosis. These facts led me to question Farmer's account of mitotic phenomena in Pallavicinia and his conception of the "quadripolar spindle," and I suggested that this structure might prove to be a phenomenon of prophase, a view to which Farmer (:01) has taken exception in a criticism of my results.

Recent investigations of Moore (:03) on Pallavicinia are flatly contradictory to the conclusions of Farmer for *Pallavicinia decipiens* and support my suggestions. Moore finds that there are two mitoses in the spore mother-cell of *Pallavicinia lyellii*, the second (Fig. 12 *c*, *d*) following immediately upon the first (Fig. 12 *b*), each with bipolar spindles and without centrosomes. The chromosomes, eight in number, appear in the usual way with each mitosis (Fig. 12 *c*, *d*). There is no "quadripolar spindle" in Farmer's sense, no quadrupling and simultaneous distribution of the chromosomes. The prophases preceding the first mitosis present a tetrahedral form as is shown in Fig. 12 *a*. This is accentuated by the fibrillae which gather at the points to make a four-rayed structure extending into the lobes of the spore mother-cell. This condition is identical with similar stages in Pellia and in other leafy liverworts, and is a feature to be expected from the fact that the spindle fibers develop chiefly or wholly externally to the nuclear membrane in a rather crowded region of the cell. The nucleus at this time is unquestionably in prophase as shown by the undifferentiated chromosomes and because this stage passes immediately into a bipolar spindle of the normal type (Fig. 12 *b*). It seems very probable that Farmer was mistaken in his conclusions for *Pallavicinia decipiens*, and that the mitoses in the spore mother-cell of this form are not different in any essentials from those of other plants.

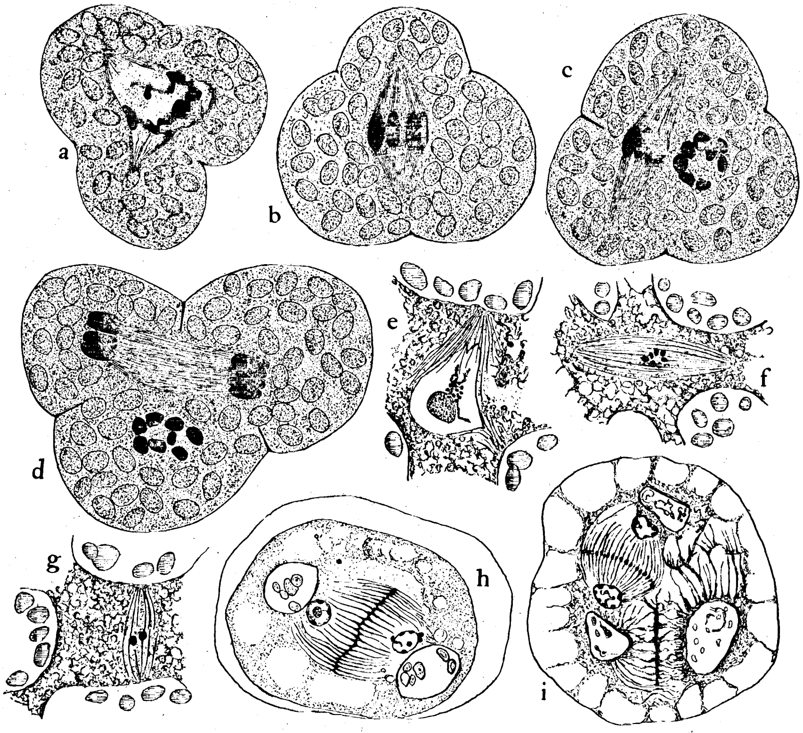

FIG. 12.— Spore mother-cells of Hepaticæ. *a, b, c, d, Pallavicinia lyellii.* *a*, Prophase; the fibrillæ gathered on four sides of the nucleus which has a tetrahedral form pointing into the four lobes of the spore mother-cell; the nuclear membrane has not yet broken down; similar stages of prophase were probably considered by Farmer as quadripolar spindles. *b*, metaphase of the first mitosis; the spindle in all respects a normal bipolar structure without centrospheres. *c*, Metaphase of the second mitosis; one spindle shown in side view, the other, almost perpendicular to the first, presents the eight chromosomes at the nuclear plate. *d*, anaphase of the second mitosis; one spindle viewed from the side, the other from one end shows the group of eight grand-daughter chromosomes. *e, f, g, anthoceros laevis, h, i*, a larger species from Italy. *e*, prophase; one pole of spindle developed. *f*, just after metaphase of the first mitosis; eight chromosomes; blunt poled spindle without centrospheres. *g*, metaphase of second mitosis; very small spindle. *h*, cell plate forming in the spindle between two nuclei. *i*, two nuclei at the side of their respective chromatophores and the cell plate between, after the second mitosis; a third chromatophore shown with strands of protoplasm connecting it with other regions of the cell. (*a, b, c, d*, after Moore, :03; *h, i*, after Van Hook, :00.)

The "quadripolar spindle" proves to be nothing more than a condition of prophase.

Besides Pellia and Pallavicinia, which are the most thoroughly studied of the lower liverworts, we know the processes of sporogenesis in the highest type, Anthoceros (Davis, '99). This form is exceedingly attractive for such investigations because the spore mother-cells may be found in all conditions upon the same sporophyte. However, the small size of the nuclei and spindles is a disadvantage. Just previous to the first mitosis the nucleus becomes surrounded by a mesh of delicate fibrillæ (kinoplasmic). Later the nucleus takes an angular form, and the fibrillæ are found conspicuously at the prominent poles (Fig. 12 *e*). The nuclear membrane breaks down and the fibers become arranged to form a bipolar spindle (Fig. 12 *f*) without centrosomes or centrospheres. There is a short period of rest after the first mitosis, but no wall is formed between the two daughter nuclei. The small spindles of the second mitosis (Fig. 12 *g*) are likewise bipolar. They lie at right angles to one another and the cell plates that are laid down determine, in part, the position of the walls that are formed between the four granddaughter nuclei and which divide the spore in a tripartite manner. These cell plates are very small (Fig. 12 *h* and *i*), but they have been observed in a favorable species of Anthoceros by Van Hook (:00). It is not clear how these plates become extended to the wall of the spore mother-cell unless (as suggested in Sec. II) their edges make use of planes of vacuoles when the protoplasm separates to develop the cleft between the four daughter cells. The poles of the spindles in Anthoceros are flattened and entirely free from structures that might be considered centrosomes.

Other interesting events of sporogenesis in Anthoceros are the division of the chromatophores and the nuclear condition termed synapsis. The young spore mother-cell contains a single large chromatophore. This increases greatly in size and becomes filled with starch grains. The chromatophore divides successively into two and then four portions which arrange themselves symmetrically in the cell with the nucleus in the center. The mitoses then follow and the four daughter nuclei are distributed, one for each chromatophore in the cell. This provision of four chromatophores long before the mitoses in the cell seems very remarkable (Davis, '99, p. 94 and 95). Synapsis is a condition very common in the nucleus of spore mother-cells before division. The chromatic material becomes gathered into a compact mass besides the nucleolus. The significance of synapsis is not clear, but the subject will be discussed in Section VI. However, there is good evidence from Anthoceros that the phenomenon is a normal event and not an artefact, because synapsis is always found at a certain period of sporogenesis, and nuclei in neighboring spore mother-cells a little older or younger present their chromatic material with the usual arrangement (Davis, '99, p. 96 and 97).

To summarize the conditions in the spore mother-cells of the Hepaticæ, all conclusions, in the author's opinion, indicate: (1) That the spindles develop from a surrounding weft of fibrillæ without the assistance of centrosomes. (2) That the mitoses are always two in number and successive with the same number of chromosomes for each division. (3) That the cell walls may be formed successively as in Pellia and some other of the Jungermanniales or simultaneously, to give tetrahedral spores, as in Anthoceros, types of the Marchantiales and Ricciales, Pallavicinia and some companion forms in the Jungermanniales. It will be interesting to note the essential agreement in these matters between the Hepaticæ and the higher plants.

Nothing is known of the nuclear activities during sporogenesis in the other great division of the bryophytes, the mosses (Musci). The spore mother-cells in this group are always small and unattractive for cell studies but the Sphagnales appear to be rather the most promising for such investigations, which are greatly to be desired.

The pteridophytes have furnished some important contributions to our knowledge of the spore mother-cell. There is first the paper of Osterhout ('97) on spindle formation in Equisetum, which was one of a group of three contributions (Mottier, '97, Juel, '97) that did much to dispose of a then prevalent belief that the development of the spindle in higher plants was controlled by centrosomes. This investigation was followed by a study of Smith (:00) on spindle formation in Osmunda. Calkins ('97) and W. C. Stevens ('98*a*) considered especially the formation and reduction of chromosomes in several of the ferns, and arrived at contradictory conclusions. Strasburger (:00, p. 76 to 79) has reviewed these results in relation to studies of his own on Osmunda.

Osterhout's ('97) account of spindle formation in Equisetum is noteworthy. He found that the nucleus of the spore mother-cell became surrounded by a web of delicate fibrillæ, which, extending radially into the surrounding cytoplasm (Fig. 13 *a*), were later (Fig. 13 *b*) gathered into numerous pointed bundles or cones. After the dissolution of the nuclear membrane these cones arranged themselves side by side in two sets to form the spindle of metaphase (Fig. 13 *c*). The spindle is then from the outset multipolar, and even though some of the cones unite when they become grouped around a common axis, nevertheless the poles of the spindle at metaphase show their composite nature in the absence of a common focal point for the fibrillæ. There are no centrosomes at the poles and no reason for their presence at any stage in the process of spindle formation.

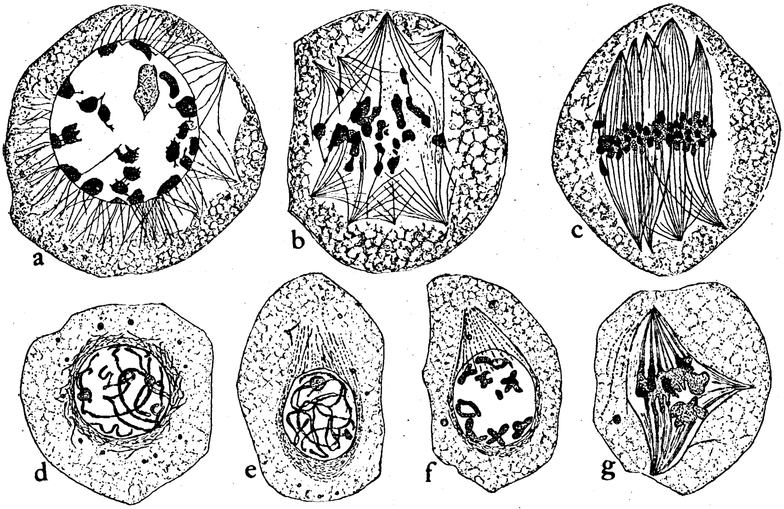

Fig. 13.— Spore mother-cells of Pteridophytes. *a, b, c, Equisetum limosum. a,* prophase of first mitosis; the radially disposed fibrillæ are gathering together into cones. *b,* prophase, older than *a*; the nuclear membrane has broken down and the fibrillæ have entered the nuclear cavity; the cones lie in two groups opposite one another. *c,* just before metaphase; the fibrillar cones are nearer together and the chromosomes have gathered to form the nuclear plate. *d, e, f, g, Osmunda regalis. d,* very early prophase of the first mitosis; nucleus in the spirem stage surrounded by a granular and fibrillar zone of kinoplasm. *e,* prophase, somewhat older than *d*; fibrillar kinoplasm showing polarity. *f,* still older; chromosomes formed; one pole of spindle developed. *g,* metaphase; a tri-polar spindle. (*a, b, c,* after Osterhout, '97; *d, e, f, g,* Smith, :00.)

Smith's (:00) study of Osmunda presents an important confirmation of Osterhout's conclusions that the spindle in pteridophytes developed without centrosomes, while illustrating a process of spindle formation along somewhat different lines. Smith distinguished a zone of kinoplasm around the nucleus previous to spindle formation. This zone became granular, and then the granules arranged themselves in rows to form fibrillæ (Fig. 13 *d*), which, however, did not extend into the cytoplasm radially, but lay generally parallel to one another, so that the spindle appeared bipolar from the beginning (Fig. 13 *e*). One pole of the spindle was generally formed considerably in advance of the other (Fig. 13 *f*). The fibers did not meet at a common point but over a broad area, and there were no centrosomes. There is, then, normally no multipolar stage in Osmunda, although tripolar spindles (Fig. 13 *g*) were occasionally found. During anaphase secondary fibers were put forth from the vicinity of the daughter nuclei and these met in the equatorial region of the cell. The spindle of the second mitosis was formed exactly as in the first. After this division the four granddaughter nuclei lay connected with one another by six spindles (two primary and four secondary). Cell plates were laid down in the equatorial regions of these spindles so that the protoplasm became divided simultaneously and symmetrically into tetrahedral spores.

The studies of Calkins ('97) and Stevens ('98*a*) were chiefly upon the division and distribution of the chromosomes in connection with reduction phenomena. Calkins believed that the processes of sporogenesis followed the same course as the maturation of sexual cells in animals, with a transverse division to give a qualitative reduction in Weismann's sense. Stevens disagreed with Calkins in several particulars, holding that the reduction was merely quantitative. Reduction phenomena in plants is now much better understood than at the time of these papers which dealt with plants much more difficult to study than some other forms (*e. g.*, types of the Liliaceæ). We shall consider the subject in Section V, but may state now that Calkins' conclusions have not been sustained.

Strasburger (:00) gives considerable attention to spindle formation in his well known review and critique of cytological literature. He proposes the following classification of spindles in higher plants which lack centrosomes. Those that pass through multipolar stages and later become bipolar are called multipolar polyarch spindles. When the spindle has a well defined axis from the beginning, as is generally true of the cells in vegetative tissues of higher plants, it is termed multipolar diarch. Strasburger has shown that these types, while easily separated in the extremes, grade into one another so that the classification is not founded on distinctions of a very fundamental character. The spindle of Osmunda, for example, resembles a multipolar diarch, but its method of development is more closely related to that of other spindles in spore mother-cells (multipolar polyarchs) than to those of vegetative tissues.

The gymnosperms offer in Larix an excellent subject for studies on the formation of pollen, and this type has been treated in several important papers, notably by Belajeff ('94*b*), Strasburger ('95) and Allen (:03). Belajeff's contribution is important as the first investigation that considered the multipolar spindle as a preliminary stage in the development of the bipolar structure. Other authors, at this time and previous to his publication, had noted multipolar and tripolar spindles (Strasburger ('80) and ('88) in several forms), but the lily had received the greatest attention in this connection (Farmer ('93) and ('95*d*), Strasburger ('95), Sargent ('97) and Mottier ('97)). Mottier's investigation presented the first detailed account of spindle formation in this angiosperm and will be discussed presently.

Allen's (: 03) paper on Larix includes one of the best discussions of the literature bearing on the subject of spindle formation that has yet appeared. He finds that the cytoplasm around the nucleus just previous to mitosis comes to contain a loose network of fibrillæ. Some of the fibers may be followed through the nuclear membrane and may be seen attached to chromatin bodies in the interior (Fig. 14 *a*). Later the cytoplasmic fibrillæ become arranged radially and extend from the nucleus even to the outer plasma membrane at the periphery of the pollen mother-cell. The radiating fibers are connected with one another by branches which indicate that the structure is in part an expanded condition of the original network, but the fibers also grow. The fibers now fold over so that they tend to lie parallel to the surface of the nucleus and thus form a dense felt around the nuclear membrane. Presently the nuclear membrane which was before a definite film becomes wavy in outline and often granular in appearance. The nucleolus shows signs of dissolution and there is a marked increase in the number of intranuclear fibers, which are chiefly or wholly of nuclear origin. After the disappearance of the nuclear membrane some of the peripheral fibers push outward to form several cones of a multipolar figure (Fig. 14 *b*). The fibers attached to the chromosomes gather into bundles that extend towards these poles. Finally the bundles of fibers become more regular and straighten out so that they come to lie approximately parallel to one another, and thus

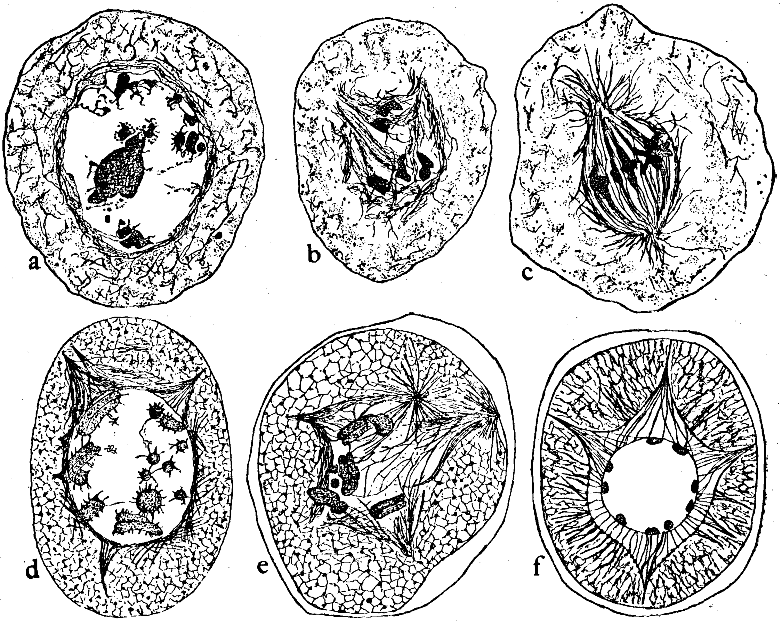

FIG. 14.— Pollen or microspore mother-cells of spermatophytes. *a, b, c, Larix europea.* *a*, prophase of first mitosis; kinoplasmic fibrillæ forming a felt around the nucleus. *b*, late prophase; the nuclear membrane has broken down and the interior space has become filled with fibrillæ which have gathered to form a multipolar spindle. *c*, metaphase; a completed spindle with polar radiations. *d, e, Lilium candidum.* *d*, prophase of first mitosis; the kinoplasmic fibrillæ have formed a net around the nucleus and are gathered into several cones which would have become poles of the spindle. *e*, late prophase; the nuclear membrane has disappeared and the fibrillæ are entering the nuclear cavity; several cones of the fibrillæ constitute the multipolar spindle. *f, Agave Americana.* Prophase of the first mitosis; the spindle cones on the upper side have pushed through the special membrane around the nucleus. (*a, b, c,* after Allen, :03; *d, e,* Mottier, '97; *f,* Osterhout, :02.)

the multipolar structure, developing a distinct axis (Fig. 14 *c*), becomes bipolar (multipolar polyarch). There is no central body at the poles and no place for a centrosome in this developmental history.

The first detailed study of spindle formation in Angiosperms was, as before stated, that of Mottier ('97) which treated especially of Lilium, Podophyllum and Helleborus. This paper with one by Juel ('97) on Hemerocallis and Osterhout ('97) on Equisetum effectually disposed of previous views very generally held (Guignard, '91, followed by other authors), that spindle formation and mitotic phenomena in higher plants was involved with the activities of centrosomes or other kinoplasmic centers. Mottier found that the nucleus in the pollen mother-cell of the lily became invested just before mitosis with radiating fibers that shortly after increased in quantity to form a felted web around the structure. Some of the fibers gathered into cones (Fig. 14 *d*) which pointed towards the periphery of the cell so that there resulted, with the disappearance of the nuclear membrane and the entrance of the fibers into the nuclear cavity, a multipolar spindle (Fig. 14 *e*). The poles gradually came to lie parallel to one another in a common axis, some of them disappearing, so that the spindle generally became distinctly bipolar at metaphase (multipolar polyarch). Essentially the same history was repeated during the second mitosis in the lily.

From this time on there have been a succession of papers verifying the general conclusions of Mottier and Juel and extending these results to many other forms until now it seems to be well established that centrosomes are never present in the pollen mother-cell and that multipolar spindles, developed from felted stages and changing to bipolar spindles, may be expected in most if not all forms. Guignard ('97 and '98) described multipolar spindles in several types (Nymphæa, Nuphar, Limodendron, etc.), and while he believed that these poles were occupied by granules that sometimes fused to form typical centrosomes, nevertheless he admitted that the multipolar spindle might be formed independently of centrosomes.

The most important papers on spindle formation in Angiosperms following those of Mottier ('97 and '98) and Juel ('97) have been Lawson ('98) on Cobea, W. C. Stevens ('98*b*) on Asclepias, Atkinson ('99) on Arisæma and Trillium, Duggar ('99) on Bignonia, Wiegand ('99) on Convallaria and Potamogeton, Gregoire ('99) on Lilium and Fritillaria, Guignard ('99) on Naias, Williams ('99) on Passiflora, Duggar (:00) on Symplocarpus and Peltandra, Lawson (:00) on Gladiolus, Byxbee (:00) on Lavatera, Andrews (:01) on Magnolia and Liriodendron, Schniewind-Thies (:01) on Galtonia and Osterhout (:02) on Agave.

Of the papers listed above several demand especial attention for the completeness of the studies on the early stages of spindle formation in the pollen mother-cell. Lawson ('98 and :00) found that the nuclei of Cobea and Gladiolus previous to mitosis were surrounded by a zone of granular kinoplasm which he named perikaryoplasm. This zone developed a felted envelope of fibrillæ from which projections extended to form the cones of a multipolar figure. The cones by fusing in two groups developed the bipolar spindles. The spindle fibers of Gladiolus are formed entirely from the perikaryoplasm, the nucleolus and linin apparently taking no part in the development of the spindle. The nucleolus remains intact until after the dissolution of the nuclear membrane when the spindle is practically completely organized. Miss Williams ('99) found for Passiflora that the nuclear cavity became filled with a network developed from the linin. The nuclear wall became also transformed into a mesh which connected the network from the linin with the surrounding cytoplasmic reticulum, thus forming a continuous system throughout the cell. The central region of this network, enclosed by a granular zone, developed a multipolar figure whose poles finally fused to form a bipolar spindle. The contrast between this type of spindle in which so much of the fibrous structure is derived from the linin and that of Gladiolus just described is very marked. A granular region outside of the fibrous network around the nucleus is much more conspicuous in Lavatera, described by Byxbee (:00), than in Passiflora. It forms in Lavatera a dense zone that suggests a gathering of nutritive material (deutoplasm). The fibrillæ are developed as a felt around the nuclear membrane and enter the nuclear cavity with the breaking down of this structure. The fibers gather into projecting cones presenting a multipolar structure, and two of these, becoming more prominent, absorb the others and thus form a bipolar spindle.

One of the most recent studies on spindle formation is that of Osterhout (: 02) on Agave. This investigation is of especial interest for the extensive experimentation in the technique of fixation. The author proposes a new terminology for the stages of mitosis that need not be presented here. Agave offers a striking peculiarity in the presence of a special membrane around the early stages of the spindle. The fibrillæ form inside of this membrane and finally push through it radially into the exterior cytoplasm where they gather into cones (Fig. 14 *f*). The cones separate into two opposite groups with a general parallel arrangement of the fibers and in this manner a bipolar spindle is formed.

It is becoming possible to make some general statements respecting the methods of spindle formation in the spore mother-cell. Just previous to prophase it is almost always possible to differentiate a region of kinoplasm around the nucleus. This zone has been found to be either granular, *e. g.*, Pellia, Anthoceros (Davis, '99 and : 01), Osmunda (Smith, : 00), Cobea and Gladiolus (Lawson, '98 and : 00), or it presents the appearance of a fibrous reticulum, *e. g.*, Equisetum (Osterhout, '97), Larix (Allen, : 03), Lilium (Mottier, '97 and '98), etc. The latter condition probably develops from the former by the arrangement of granules into fibers and the gradual expansion of a very close network thus formed into a coarser structure. The fibers in this reticulum sometimes surround the nucleus as with a heavy web. They later extend radially into the cytoplasm, partly by the expansion of the network and partly by their own growth and frequently take a radial arrangement. In some instances the spindle fibers are developed very largely within the nucleus from the linin (Passiflora, Williams, '99). They then become gathered into bundles or groups forming the cones which collectively constitute a multipolar figure that is often called a multipolar spindle. By the rearrangement of these cones somewhat parallel to one another, together with more or less fusion, the multipolar structure becomes a bipolar spindle (multipolar polyarch) generally just previous to the period of metaphase. The formation of cell plates and the disappearance of the spindle fibers have been discussed in Section II under the title "Cleavage by cell plates."

Mention should be made of some irregularities in the division and distribution of the chromosomes that are conspicuous in certain spore mother-cells and which have been the cause of much discussion. The subject has especial reference to certain older views of the reduction phenomena in plants. Chromosomes split once longitudinally in all typical mitoses and the halves are drawn apart in a symmetrical manner which is very easily understood. This division is really determined by the longitudinal fission of the spirem thread. But appearances during the first nuclear division in the spore mother-cell of many forms have puzzled investigators for many years and have given rise to a number of interpretations. It seems to be pretty clearly established now that in these types there is a double longitudinal splitting of the chromosomes at the time of this mitosis. The first division takes place during prophase and the second follows closely after the first and is generally clearly seen at metaphase or during anaphase. Therefore the chromatic bodies which appear at the nuclear plate during the first mitosis are in reality divided or about to be divided into quarters and they separate after this mitosis as pairs of granddaughter chromosomes instead of simple daughter elements. These pairs are either firmly united at one end into a V or irregularly drawn out so that the bodies have very unusual and sometimes bizarre forms. Nuclear figures of this irregular appearance were originally described by Flemming for the first mitosis in the spermatocyte of Salamandra and named by him "heterotypic." These in the spore mother-cell of plants are of similar character and the designation "heterotypic" has been adopted by botanists for this condition. The pairs of chromosomes that enter the daughter nuclei after the first mitosis fuse end to end to form a spirem thread which breaks up again during the second mitosis, without longitudinal fission, into pairs of chromosomes which are believed to be identical with those that entered the nucleus after the first mitosis. Since there is no longitudinal splitting of the spirem thread before the second division this mitosis differs from that of the "typical" mitoses of cells and is called "homotypic" to distinguish it on the one hand from the former and on the other from "heterotypic" divisions. Several illustrations of heterotypic and homotypic mitoses to be described presently are presented in Fig. 15, showing the peculiar V-shaped pairs of granddaughter chromosomes, characteristic of the first group. It is important to note that whatever the significance of this premature fission of the chromosomes before the second mitosis it is not of the nature of a qualitative reduction division in Weisman's sense. The details and significance of reduction phenomena will be considered in other connections (Section V). The topics discussed above have been recently studied and reviewed by Mottier (:03).

We have as yet said nothing of the megaspore mother-cell in Spermatophytes. An increasing number of investigations have clearly established the fact that the embryo-sac in many forms is one of a group of two, three or four cells, each of which is a potential megaspore because its nucleus contains the reduced number of chromosomes. We are accustomed to think of the well known conditions in the lily, where the megaspore mother-cell develops directly into the embryo-sac. But this type with some others (*e.g.*, Fritillaria, Tulipa, Erythronium, etc.) are the exceptions and present a very highly differentiated condition in which the usual developmental history is shortened in a very interesting manner, which will be described presently.

The embryo-sac arose undoubtedly as one of four megaspores developed after essentially the same manner as microspores or pollen grains, excepting that their arrangement was generally in a row, which is even true of some pollen grains (*e. g.*, Asclepias, Zostera). As stated above, an increasing number of investigations have established the row of four potential megaspores in a large number of forms in various groups. They may not always be distinguished by the form of the group, but their homologies are established by the mitoses that lead to their differentiation. Two mitoses are of course required to establish the group of four cells and both are identified by the reduced number of chromosomes. Some detailed studies on these mitoses have established the fact for certain forms that the first is heterotypic and the second homotypic, exactly as in divisions of the microspore or pollen mother-cells. Schniewind-Thies (: 01) figures very completely the mitoses in Galtonia. The first mitosis in the megaspore mother-cell (Fig. 15*a*) is heterotypic because the

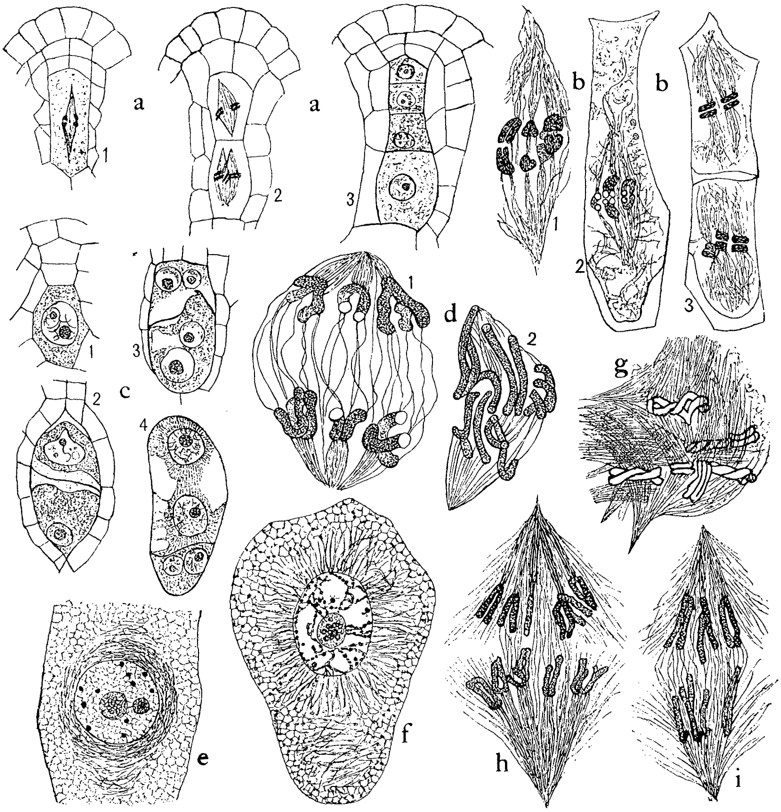

Fig. 15.— Embryo sac or megaspore mother-cell of spermatophytes. *a*, *b*, *Galtonia candicans*. *a*1, first mitosis in megaspore mother-cell. *a*2, second mitosis. *a*3, group of four megaspores. *b*1 and *b*2, shortly after metaphase of the first mitosis (heterotypic). *b*3, metaphase of the second mitosis (homotypic). *c*, *d*, *Scilla Sibirica*. *c*1, megaspore mother-cell. *c*2, after the first mitosis. *c*3, after the second mitosis, the lower cell of the pair to become the embryo sac. *c*4, after the second mitosis, the upper cell of the pair to become the embryo sac. *d*1, anaphase of the first mitosis (heterotypic). *d*2, anaphase of the second mitosis (homotypic). *e*, *Lilium martagon*; portion of embryo sac mother-cell, nucleus surrounded by a felt of fibrillæ. *f*, *Lilium candidum*: embryo sac mother-cell, nucleus surrounded by radiating fibrillæ. *g*, *h*, *i*, *Lilium martagon*. *g*, late prophase of first mitosis in embryo sac mother-cell, a multipolar spindle. *h*, anaphase of first mitosis (heterotypic). *i*, anaphase of second mitosis (homotypic). (*a*, *b*, *c*, *d*, after Schniewind-Thies : 01 ; *e*, *f*, *g*, *h*, *i*, Mottier '97.)

chromosomes (Fig. 15*b*, 1, 2) show clearly the V-shaped forms characteristic of this division. The second mitosis (Fig. 15 *b*, 3) is homotypic. The lowest cell of the group of four (Fig. 15 *a*, 3) becomes the embryo-sac and the mitoses that take place within it as the female gametophyte develops are all typical. This account illustrates a simple history in megaspore mother-cell development and is considered the first of three types in a classification proposed by Schniewind-Thies (:01).

The second type of development is one in which two megaspores are generally developed from a mother-cell and one of these becomes the functional embryo-sac. Schniewind-Thies presents an excellent illustration of this type in Scilla. The first mitosis in the megaspore mother-cell (Fig. 15 *c*) is heterotypic (Fig. 15 *d*, 1) and results in two cells (Fig. 15 *e*). The second mitosis in both cells is homotypic (Fig. 15 *d*, 2). Either the lower (Fig. 15 *e*, 3) or the upper (Fig. 15 *e*, 4) of the pair may become the embryo-sac. The embryo-sac then includes the homotypic or second mitosis within its development, making it the first nuclear division of the gametophyte history. The typical mitoses of the gametophyte begin with the second nuclear division in the embryo-sac. Three megaspores may be formed in such a group when the cell of the pair that does not become the embryo-sac divides again.

The third type of development is illustrated by several forms, of which the best known are Lilium (Mottier, '98 and :03) and Tulipa (Schniewind-Thies :01). The lily has been much studied, but Mottier presents the most detailed account of spindle formation and the behavior of the chromosomes. He supports the observations of Schniewind-Thies, based upon the tulip, and her explanation of this type of development. The megaspore mother-cell of the lily and tulip develops directly into the embryo-sac. The first mitosis in this cell (Fig. 15 *h*) is heterotypic and the second (Fig. 15 *i*) homotypic. These divisions give the four-nucleate embryo-sac and one more mitosis presents the mature structure. This last is a typical mitosis, the only one found in the embryo-sac before the development of the endosperm and sporophyte embryo. Thus the two mitoses characteristic of the spore mother-cell are here included within the embryo-sac and appropriated as a part of the gametophyte history.

We can see in these three types of embryo-sac development an evolutionary process of which the third stage is plainly derived from the simpler second and first, and is consequently a highly developed and very complex condition, far removed from primitive gametophyte structures among the angiosperms. The embryo-sacs of these forms (Lilium, Tulipa, Fritillaria, Erythronium, etc.) are probably the most complex spore mother-cells that we know. The studies of Schniewind-Thies and Mottier have been supported by other investigations, and more especially by the results of Ernst (: 02) on *Paris quadrifolia* and *Trillium grandiflorum*, who followed the history of the heterotypic and homotypic mitoses in these forms in detail. They illustrate the second type of embryo-sac development in the classification of Schniewind-Thies.

Spindle formation in the embryo-sac mother-cell has not received as much attention as in the pollen mother-cell, probably because material of the latter structures may be obtained much more readily than the former. There have been numerous descriptions and figures of the spindles but few accounts in full of their development. Of the latter the investigation of Mottier ('98) on Lilium is the most complete. This paper was written at the time when the centrosome question was under discussion and served, with other papers on the spore mother-cell (Osterhont, '97, Juel, '97, Mottier, '97) to discredit the presence of these bodies in this structure. Mottier found that the nucleus of the embryo-sac became invested with a close network of fibrillæ (Fig. 15 *e*) from which fibers developed into the cytoplasm radiating from the nucleus in all directions (Fig. 15 *f*). With the dissolution of the nuclear membrane the fibrillæ entered the nuclear cavity, filling it with masses of fibers which gathered into cones to form a complicated multipolar spindle (Fig. 15 *g*). These cones later come together into two poles, but even in the mature spindle the fibrillæ are frequently in several groups at the poles. Essentially the same history is repeated in the second mitosis. A large number of later papers have described and figured multipolar spindles in embryo-sacs, confirming the conclusions of Mottier that these structures are developed here after the same methods as in the pollen mother-cell, from surrounding investments of fibrillæ and without centrosomes. Indeed the embryo-sac is remarkable for the quantity of the cytoplasmic fibrillæ present during its mitoses.

In concluding this account attention should be called to some forms whose microspore mother-cells were formerly supposed to omit the mitoses of sporogenesis and develop directly into pollen grains. These conditions were reported in Zostera, the Cyperaceæ, and the Asclepiadaceæ. However, Juel (:00) finds the two mitoses present in *Carex acuta*, although three of the nuclei break down and the cytoplasm is appropriated for the fourth to form a single pollen grain whose wall is developed from that of the mother cell. The history is very similar to the development of the megaspore in certain heterosporous pteridophytes (*e.g.*, Marsilia, Selaginella) and to the embryo-sac, which functions while its companion polential megaspores degenerate. The development of the pollen in the Asclepiadaceæ has been shown to be normal in the nuclear activities by several investigators (Frye, :01, Strasburger, :01, and Gagner, :02), the tetrad consisting of four pollen grains in a row, instead of the usual arrangement. In Zostera (Rosenberg, :01) there are longitudinal divisions of the very much elongated pollen mother-cell to give four extraordinary filiform pollen grains.

5. The Cœnocyte.

This remarkable type of cell has reached an extraordinarily high state of development in certain plants, notably among the Siphonales and the filamentous Phycomycetes (Mucorales, Saprolegniales and Peronosporales). Cœnocytes are multinucleate cells. The simplest types are developed by the limited division or fragmentation of a nucleus accompanied by an increase in the size of the cell but without extended growth. Excellent illustrations are found in the older cells of the red algæ, the internodal cells of the Characeæ and in old parenchyma cells of many higher plants.

A higher type of cœnocyte is presented when the multinucleate cells show some definite activity resulting in extensive growth or peculiarity of form. Thus some laticiferous cœnocytes are branching tubes that grow for considerable distances among the cells of the tissues in which they are contained. The embryo-sac and the female gametophytes of Selaginella and Isœtes in the early stages of their development are interesting cœnocytes. Among the lower algæ there are numbers of cœnocytic forms (*e. g.*, Hydrodictyon, Cladophora) whose cells present very little change with age except an increase in size. Yet some of these conditions, especially those illustrated in the Cladophoraceæ, are probably related to the higher types of cœnocytes.

The best differentiated cœnocytes are found in the Siphonales, Mucorales, Saprolegniales and to a lesser extent among the Peronosporales and are especially well illustrated in a few aquatic forms, such as Monoblepharis and Myrioblepharis. The peculiarities of these forms lie in elaborate structures which result from the ability of the cœnocyte to respond to several directive stimuli in its growth. The most complicated responses and consequently the most highly differentiated morphology is shown among the Siphonales, where some very elaborate forms are found. In many types the plant body is clearly composed of root and shoot regions and in the highest expressions (*e. g.*, some species of Caulerpa) there are rhizoids, shoots and leaf-like structures presenting a remarkable degree of specialization. The behavior of the protoplasm in these most highly differentiated types of the Siphonales is known to us chiefly through studies of Noll and Klemm.

There is a very conspicuous layer of clear protoplasm next to the cell wall which constitutes an outer plasma membrane (hautschicht). This outer plasma membrane is stationary while the granular protoplasm within changes its position readily and frequently in different portions of the plant streaming in various directions. The nuclei are all situated in the granular cytoplasm so that they must shift their positions with its movements. Noll ('87) by a clever method of coloring the cell wall of living plants of Caulerpa was able to prove that the forward growth took place by the protoplasm extending beyond the old wall, thus adding new regions of cellulose to the old. He called this method of growth a process of eruption in contrast to Nägeli's conception of growth by intussusception. Increase in thickness comes with the laying down of successive lamellæ inside the older wall and is consequently growth by apposition. Caulerpa is very favorable for such investigations and Noll's results greatly strengthen the theory that a cellulose wall results from the direct transformation of a plasma membrane in which carbohydrate molecules gradually replace those of albuminous material. Accordingly the cellulose wall is not strictly a secretion and its growth is not by the intercalation of new molecules among the old (intussusception) in a non-living membrane.

The wide space in the interior of the filaments of Caulerpa and some other members of the Siphonales is frequently crossed by cellulose bars at various angles. These are at first strands of protoplasm which become gradually filled with a carbohydrate material and finally solidified. Noll ('88*a*), while recognizing that these structures may have value in strengthening the filament, believes that they are also the paths of metabolic exchange between the interior regions of the protoplasm and the water outside the plant. They are surrounded by the plasma membrane which in consequence presents a much greater extent of surface to the water permeating the cell wall.

It is plain that because of the constant movement of the granular cytoplasm carrying with it the nuclei which change their position in the cell, the outer plasma membrane is the only portion of the protoplasm that can receive fixed stimuli for an extended period. Consequently Noll regards this membrane as the responsive or irritable region of the cell that reacts to the stimuli which largely or wholly direct growth. Some of these stimuli are well established. Thus it is light which directs the formation of leaves and shoots. The behavior of Caulerpa in relation to prominent stimuli (light, darkness, gravity, etc.) has been studied by Noll ('88*b*) and Klemm ('93). The latter author believes that the response is due to the presence of foods or other substances at certain points which make them especially sensitive to the external stimuli. Injuries to a filament of the Siphonales brings about an immediate flow of protoplasm to the wounded part (Klemm,' 94), after which the plasma membrane is quickly repaired and new portions of the wall laid down.

Mitotic phenomena in the Siphonales is known to us only through the investigations of Fairchild ('94) on Valonia. He found that nuclei in the same individual may divide directly or indirectly. The first process is one of simple fission, the latter takes place with the formation of an intranuclear spindle. Studies in sporogenesis and gametogenesis are very much to be desired in the Siphonales that we may understand the behavior of the nuclei at these periods. The author's recent studies of oögenesis in Vaucheria (Davis, :04*a*) have shown an interesting process of nuclear degeneration similar to that in the Saprolegniales and Peronosporales, and suggests some very interesting lines of investigation.

The protoplasmic structure in the hyphæ of the larger filamentous Phycomycetes, especially the Saprolegniales and Peronosporales, is undoubtedly much the same as in the Siphonales. But the absence of chlorophyll and the greater delicacy of the filaments makes it more difficult to recognize the different regions of the protoplasm. There is an outer plasma membrane inside of which the granular material slowly moves in protoplasmic currents that may sometimes be observed in rapidly growing tips. Delicate strands which are the paths of streaming currents are beautifully shown in developing sporangia of the molds and the oögonia of the Saprolegniales and Peronosporales. The nuclei are undoubtedly carried by the protoplasmic movements, sometimes collecting in cnnsiderable numbers in growing regions of the filaments which always contain much dense protoplasm.

Another type of cœnocyte, and in some respects the most remarkable, is the plasmodium of the Myxomycete. These structures are too well known to need description here. We shall only refer to them as they help to break down an old theory that the cœnocyte is a compound structure composed of many energids, represented by the nuclei, which coöperate to make up the whole. The plasmodium and the protoplasmic mass inside the cellulose tubes of the Siphonales and Phycomycetes agree in all essentials of structure and mode of growth. The forward growth of the plasmodium, as is also true of the Amœba, begins with the prolongation of the outer plasma membrane (hautschicht, ectoplasm) into a process (pseudopodium) which advances and is followed immediately by an inflow of the granular cytoplasm. And the growth of the filaments of the Siphonales and higher Phycomycetes is a pushing forward of the outer plasma membrane followed by the granular protoplasm, but this growth is slow because the plasma membrane is at all times under the restraint of a cellulose envelope.

Mention should be made of the remarkable cœnocytic zoöspores well known in Vaucheria and also described by Thaxter ('95*b*), for the Phycomycete Myrioblepharis. In Vaucheria the entire contents of the sporangium becomes transformed into an immense multinucleate zoöspore, the cilia being distributed in pairs above the nuclei. In Myrioblepharis the contents of a sporangium usually forms four large multiciliate zoöspores.

These zoöspores of Vaucheria have often been called compound zoöspores, and the idea has been expressed that they stand for the coöperative union of many hundreds of zoöspores (energids) represented by the nuclei and their respective pairs of cilia. And this explanation of the zoöspore of Vaucheria is a part of a broad view, formerly very largely held, that the cœnocyte is an assemblage of energids (uninucleate masses of protoplasm) coöperating in a fused structure.

The theory of the coöperative association of energids in a cœnocyte (Sachs) has been very much modified. While the nucleus and some other organs of the cell, such as groups of cilia, plastids, etc., are homologous with the same structures in uninucleate cells nevertheless the behavior of the cœnocyte is not the same as a group of coöperating protoplasmic units. The cœnocyte reacts to the usual stimuli in precisely the same manner as a uninucleate cell, and must be regarded as physiologically presenting no peculiarities over the latter structure excepting those of an increased bulk of protoplasm demanding a greater number of nuclei for its metabolic processes. The most important contribution presented by the cœnocyte to our knowledge of the physiology of the cell is the establishment of the plasma membrane as the region of the protoplasm responsive to the stimuli that determine the form assumed in growth. The constant shifting of the nuclei and plastids in the movement of the granular protoplasm eliminates them as structures immediately concerned with the form of a cell or organ thus limiting their functions more especially to metabolism.

6. The Cœnogamete.

The cœnogamete is a multinucleate sexual cell. The name was first applied by the author (Davis, :00, p. 307) to the remarkable multinucleate eggs of *Albugo bliti*, and the conception has been considerably extended since, as explained in his later writings on Saprolegnia (Davis, :03, p. 320–331) and on "The relationships of sexual organs in plants" (Davis, :04*b*). Stevens ('99) discovery of the multinucleate eggs of *Albugo bliti* opened a field of research that has been greatly extended in the past four years and which is likely to yield very important conclusions on the relationships and evolution of the Phycomycetes and Ascomycetes. Conditions similar to *Albugo bliti* were reported the following year by Harper, :00*b*, for Pyronema, and several later papers have described, with greater or less fullness, the structure and behavior of cœnogametes in some other Ascomycetes, types of the Peronosporales (species of Albugo) and in the Mucorales.

We shall not discuss the details of these investigations with their bearings upon the problems of phylogeny as this has become a very complicated subject and is treated elsewhere (Davis, :04 *a–b*), but merely describe the structure and behavior of cœnogametes so far as they are known to us.

Stevens and Harper both found that the multinucleate female cell of *Albugo bliti* and Pyronema was fertilized by the introduction of a large number of nuclei from the antheridium. These sexual nuclei paired off and fused, a male with a female, in the common mass of cytoplasm so that the fertilized cell finally contained a large number of fusion nuclei. A similar history was reported later by Stevens (:01), in *Albugo portulacae* and *Albugo tragopogonis*. These events have been so thoroughly studied that we know the processes of fertilization in the above forms as well perhaps as for any plant type.

The structure and especially the nuclear history of other cœnogametes is less perfectly understood. The multinucleate character of the fusing gametes is well known, but the later distribution and fate of the sexual nuclei has not been followed, and it is by inference that we believe these cœnogametes to behave in essentially the same manner as those of Albugo and Pyronema.

Cœnogametes fall into two classes according as they involve all of the protoplasm contained within the mother-cell or only a portion of such protoplasm. The first group probably represents the simplest and most primitive conditions.

Cœnogametes of the first class are found in the Mucorales (Gruber : 01) and in the Gymnoasceæ (Dale, : 03). In these types the entire contents of the terminally formed sexual cells unite to produce the zygospore in the former group and the fertilized ascogonium in the latter, from which arises the system of ascogenous hyphæ.

Cœnogametes of the second class contain only a portion of the protoplasm in the mother-cell which is usually a terminal structure. The protoplasm that is not involved in the cœnogamete proper generally bears some important relation to the sexual element. Thus the periplasm of the Peronosporales assists in the formation of the wall of the oöspore and the conjugation tube of Pyronema becomes the path through which the contents of the antheridium enters the ascogonium. But in some forms the superfluous protoplasm is merely cut off from the cœnogamete as a sterile cell (Monascus). In Albugo and Pyronema the sterile and fertile portions of the protoplasm are so closely associated that the mother-cell really acts as a whole, very much as the simplest types of cœnogametes which shows the close relationships between the two. Moreover the antheridia of these forms are types of cœnogametes almost as simple as those of the molds or the Gymnoasceæ.

The cœnogamete is a type of sexual cell unknown in the animal kingdom and among plants is probably restricted to the Phycomycetes and Ascomycetes. The problems of its homologies and origin are very interesting.

The simplest types of cœnogametes (Mucorales and Gymnoasceæ) are cells situated at the ends of filaments in the same position as the sexual organs of the Siphonales. The mother-cells of the more complicated cœnogametes (oögonia and antheridia) are also terminal cells. All of these sexual organs are multinucleate. In the Siphonales (Vaucheria excepted) all of the nuclei are functional gamete nuclei. This is also true of simplest types of cœnogametes, but in the more complicated forms (Albugo, Pyronema, etc.) large numbers of the nuclei degenerate or fail to function sexually in sterile accessory regions of the protoplasm. The same conditions of sexual degeneration are also found in the oögonia of Vaucheria (Davis, :04) and Saprolegnia (Davis, :03). The agreement of all of the structures mentioned above in structure and protoplasmic behavior seems to establish beyond question their common homology.

The problems of the origin of the cœnogametes are very difficult with the meager evidence at hand. The author believes that the simplest types have probably been derived from structures like the sexual organs of the isogamous Siphonales, which structures gave up the habits of forming uninucleate gametes and acting as cœnocytic units became multinucleate sexual elements. A physiological development very similar to such a change must have taken place in Peronospora and some species of Pythium when their conidia ceased forming zoöspores and took the habit of germinating directly by a tube. This view regards the cœnogamete as a cœnocyte derived from a protoplasmic structure that at one time produced a large number of independent sexual elements, represented in the cœnocyte by the numerous nuclei. Whether the higher types of cœnogametes (Albugo, Pyronema, etc.) have developed directly from the simpler forms or from levels of the heterogamous algæ, such as are illustrated by Vaucheria, are very complicated problems that cannot be treated here. They with other topics, mentioned above, have been considered in recent papers of the author (Davis, :03, ;04*a*, :04*b*). Cœnogametes are proving to be among the most interesting types of sexual cells in plants and research in this field is likely to prove very fruitful of results.

LITERATURE CITED FOR SECTION III. "THE PLANT CELL."

ALLEN.

:**03**. The early stages of spindle formation in the pollen mother-cell of Larix. Ann. of Bot. **17**, 281.

ANDREWS.

:**01**. Karyokinesis in Magnolia and Lirodendron. Bot. Centb. Beihefte **11**, 134.

ARNOLDI.

:**00***a*. Embryogenie von Cephalotaxus fortunei. Flora **87**, 46.

ARNOLDI.

:**00***b*. Was sind die Keimbläschen oder Hofmeisters–Körperchen in der Eizelle der Abietineen. Flora **87**, 194.

ATKINSON.

'**99**. Studies on reduction in plants. Bot. Gaz. **28**, 1.

BELAJEFF.

'**94***a*. Ueber Bau und Entwickelung der Spermatozoiden der Pflanzen. Flora **79**, 1.

BELAJEFF.

'**94***b*. Zur Kenntniss der Karyokinesis bei den Pflanzen. Flora **79**, 430.

BELAJEFF.

'**97***a*. Ueber den Nebenkern in spermatogenen Zellen und die Spermatogenese bei den Farnkrauter. Ber. d. deut. bot. Gesell. **15**, 337.

BELAJEFF.

'**97***b*. Ueber Spermatogenese bei den Schachthalmen. Ber. d. deut. bot. Gesell. **15**, 337.

BELAJEFF.

'**97***c*. Ueber die Aehnlichkeit einiger Erscheinungen in der Spermatogenese bei Thieren und Pflanzen. Ber. d. deut. bot. Gesell. **15**, 342.

BELAJEFF.

'**98**. Ueber die Cilienbildner in den spermatogenen Zellen. Ber. d. deut. bot. Gesell. **16**, 140.

BELAJEFF.

'**99**. Ueber die Centrosomen in den spermatogenen Zellen. Ber. d. deut. bot. Gesell. **17**, 199.

BLACKMAN.

'**98**. The cytological features of fertilization and related phenomena in Pinus silvestris L. Phil. Trans. Roy. Soc. **190**, 395.

BYXBEE.

:**00**. The development of the karyokinetic spindle in the pollen mother-cells of Lavatera. Proc. Cal. Acad. Sci. Bot. III, **2**, 63.

CALKINS.
'97. Chromatin reduction and tetrad-formation in Pteridophytes. Bull. Tor. Bot. Club, **24**, 101.

CAMPBELL.
'88. The development of Pilularia globulifera. Ann. of Bot. **2**, 233.

CAMPBELL.
'91. Contributions to the life history of Isoetes. Ann. of Bot. **5**, 231.

CAMPBELL.
'92*a*. On the prothallium and embryo of Osmunda clatoniana, L. and O. cinnamomea, L. Ann. of Bot. **6**, 49.

CAMPBELL.
'92*b*. On the prothallium and embryo of Marsilia vestita. Proc. Cal. Acad. Sci. II, **3**, 183.

CAMPBELL.
'94. Observations on the development of Marattia douglasii, Baker. Ann. of Bot. **8**, 1.

CHAMBERLAIN.
'99. Oögenesis in Pinus laricio. Bot. Gaz. **27**, 268.

COKER.
:02. Notes on the gametophytes and embryo of Podocarpus. Bot. Gaz. **33**, 89.

COKER.
:03. On the gametophytes and embryo of Taxodium. Bot. Gaz. **36**, 1 and 114.

DALE.
:03. Observations on the Gymnoasceae. Ann. of Bot. **17**, 571.

DANGEARD.
'99. Memoire sur les Chlamydomonadinees ou l'histoire d'une cellule. Le Bot. VI, 65.

DANGEARD.
'01. Etude sur la structure de la cellule et ses functions, Le Polytoma uvella. Le Bot. VIII, 5.

DAVIS.
'99. The spore mother-cell of Anthoceros. Bot. Gaz. **28**, 89.

DAVIS.
:00. The fertilization of Albugo candida. Bot. Gaz. **29**, 297.

DAVIS.
:01. Nuclear studies in Pellia. Ann. of Bot. **15**, 147.

DAVIS.
:03. Oögenesis in Saprolegnia. Bot. Gaz. **35**, 233 and 320.

DAVIS.
:04*a*. Oögenesis in Vaucheria. Bot. Gaz. **38**, 81.

DAVIS.
:04*b*. The relationships of sexual organs in plants. Bot. Gaz. **38**, 243.

DIXON.

'**94**. Fertilization of Pinus sylvestris. Ann. of Bot. **8**, 21.

DUGGAR.

'**99**. On the development of the pollen grain and embryo-sac in Bignonia venusta. Bull. Tor. Bot. Club, **26**, 89.

DUGGAR.

:**00**. Studies in the development of the pollen grain in Symplocarpus fœtidus and Peltandra undulata. Bot. Gaz. **29**, 81.

ERNST.

:**02**. Chromosomenreduction, Entwickelung des Embryosackes und Befruchtung bei Paris quadrifolia L. und Trillium grandiflorum Salisb. Flora, **91**, 1.

FAIRCHILD.

'**94**. Ein Beitrag zur Kenntniss der Kerntheilung bei Valonia utricularia. Ber. d. deut. bot. Gesell. **12**, 331.

FARMER.

'**93**. On nuclear division in the pollen mother-cells of Lilium martagon. Ann. of Bot. **8**. 392.

FARMER.

'**94**. Studies in Hepaticae: On Pallavicinia decipiens Mitten. Ann. of Bot. **8**, 35.

FARMER,

'**95***a*. Spore formation and karyokinesis in Hepaticæ. Ann. of Bot. **9**, 363.

FARMER.

95*b*. On spore formation and nuclear division in the Hepaticæ. Ann. of Bot. **9**, 469.

FARMER.

'**95***c*. Further investigations on spore formation in Fegatella conica. Ann. of Bot. **9**, 666.

FARMER.

'**95***d*. Ueber Kerntheilung in Lilium-antheren, besonders in Bezug auf die Centrosomenfrage. Flora, **80**, 56.

FARMER.

:**01**. The quadripolar spindle in the spore mother-cell of Pellia epiphylla. Ann. of Bot. **15**, 431.

FERGUSON.

:**01***b*. The development of the egg and fertilization in Pinus strobus. Ann. of Bot, **15**, 435.

FRYE.

:**01**. Development of the pollen in some Asclepiadaceæ. Bot. Gaz. **32**, 325.

GAGNER.

:**02**. The development of the pollinium and sperm cells in Asclepias Cornuti, Decaise. Ann. of Bot. **16**, 123.

GREGOIRE.
'99. Les cineses polliniques chez les Liliacées. La Cellule **16**, 325.

GRUBER.
:01. Ueber das Verhalten der Zellkerne in den Zygosporen von Sporodinia grandis Link. Ber. d. deut. bot. Gesell. **19**, 51.

GUIGNARD.
'91. Nouvelles études sur la fecondation. Ann. d. Sci. Nat. Bot. VII, **14**, 163.

GUIGNARD.
'97. Les centres cinétiques chez les végétaux. Ann. d. Sci. Nat. Bot. VIII, **6**, 177.

GUIGNARD.
'98. Centrosomes in Plants. Bot. Gaz. **25**, 158.

HARPER.
:00*b*. Sexual reproduction in Pyronema confluens and the morphology of the ascocarp. Ann. of Bot. **14**, 321.

HIRASE.
'94. Notes on the attractions-spheres in the pollen-cells of Ginko biloba. Bot. Mag. Tokyo **8**, 359.

HIRASE.
'97. Untersuchungen über das Verhalten des Pollens von Ginko biloba. Bot. Centb. **69**, 33.

HIRASE.
'98. Etude sur la fecondation et l'embryogenie du Ginko biloba. Jour. Coll. Sci. Imp. Tokyo, **12**, 103.

IKENO.
'98*a*. Zur Kenntniss des sogenanten centrosomähnlichen Körpers im Pollenschlauch der Cycadeen. Flora **85**, 15.

IKENO.
'98*b*. Untersuchungen über die Entwickelung der Geschlechtsorgane und den Vorgang der Befruchtung bei Cycas revoluta. Jahrb. f. wiss. Bot. **32**, 557.

IKENO.
:01. Contribution a l'etude de la fecondation chez le Ginko biloba. Ann. d. Sci. Nat. VIII, **13**, 305.

IKENO.
:03. Beiträge zur Kenntniss der pflanzlichen Spermatogenese: Die Spermatogenese von Marchantia polymorpha. Beitr. z. bot. Centb. **15**, 65.

JUEL.
'97. Die Kerntheilung in den Pollenmutterzellen von Hemerocallis fulva und die bei denselben auftretenden Unregelmassigkeiten. Jahrb. f. wiss. bot. **30**, 205.

JUEL.
:00. Beiträge zur Kenntniss der Tetradentheilung. Jahrb. f. wiss. Bot. **35**, 626.

KARSTEN.
'92. Beiträge zur Entwickelungsgeschichte der Gattung Gnetum. Bot. Zeit. **50**, 205, 221 and 237.
KARSTEN.
'93. Zur Entwickelungsgeschichte der Gattung Gnetum. Cohns Beit. z. Biol. d. Pflan. **6**, 337.
KLEBAHN.
'92. Die Befruchtung von Oedogonium boscii. Jahrb. f. wiss. Bot. **24**, 235.
KLEMM.
'93. Ueber Caulerpa prolifera. Flora, **77**, 460.
KLEMM.
'94. Ueber die Regenerationsvorgänge bei den Siphonaceen. Flora, **78**, 19.
LAND.
:02. A morphological study of Thuja. Bot. Gaz. **34**, 249.
LAWSON.
'98. Some observations on the development of the karyokinetic spindle in the pollen mother-cell of Cobea scandens. Proc. Cal. Acad. Sci. Bot. III. **1**, 169.
LAWSON.
:00. Origin of the cones of the multipolar spindle in Gladiolus. Bot. Gaz. **30**, 145.
LOTSY.
'99. Contributions to the life history of the genus Gnetum. Ann. Jar. Bot. Buiten. II, **1**, 46.
LYON.
:01. A study of the sporangia and gametophytes of Selaginella apus and Selaginella rupestris. Bot. Gaz. **32**, 131.
MIYAKE.
:03*a*. On the development of the sexual organs in Picea excelsa. Ann. of Bot. **17**, 351.
MIYAKE.
:03*b*. Contribution to the fertilization and embryogeny of Abies balsamea. Beitr. z. Bot. Centb. **14**, 134.
MOORE.
:03. The mitoses in the spore mother-cell of Pallavicinia. Bot. Gaz. **36**, 384.
MOTTIER.
'97. Beiträge zur Kenntniss der Kerntheilung in den Pollenmutterzellen einiger Dikotylen und Monokotylen. Jahrb. f. wiss. Bot. **30**, 169.
MOTTIER.
'98. Ueber das Verhalten der Kerne bei der Entwickelung des Embryosacks und die Vorgänge bei der Befruchtung. Jahrb. f. wiss. Bot. **31**, 125.

MOTTIER.

:03. The behavior of the chromosomes in the spore mother-cells of higher plants and the homologies of the pollen and embryo-sac mother-cell. Bot. Gaz. **35**, 250.

MURRILL.

:00. The development of the archegonium and fertilization in the hemlock spruce (Tsuga Canadensis Carr.) Ann. of Bot. **14**, 583.

NOLL.

'87. Experimentelle Untersuchungen uber das Wachsthum der Zellmembran. Abhand. d. Senc Kenberg. naturf. Gesell. **15**, 101.

NOLL.

'88*a*. Ueber die Function der Zellstoffasern der Caulerpa prolifera. Arbeit. a. d. bot. Inst. Würz. **3**, 459.

NOLL.

'88*b*. Ueber den Einfluss der Lage auf die morphologische Ausbildung einiger Siphoneen. Arbeit a. d. bot. Inst. Wurz. **3**, 466.

OLTMANNS.

'95. Ueber die Entwickelung die Sexualorgane be Vaucheria. Flora, **80**, 388.

OLTMANNS.

'98. Die Entwickelung der Sexualorgane bei Coleochæte pulvinata. Flora, **85**, 1.

OSTERHOUT.

'97. Ueber Entstehung der karyokinetischen Spindel bei Equisetum. Jahrb. f. wiss. Bot. **30**, 159.

OSTERHOUT.

:02. Spindle formation in Agave. Proc. Cal. Acad. Sci. Bot. **2**, 255.

PRINGSHEIM.

'58. Morphologie der Oedogonieen. Jahrb. f wiss. Bot. **1**, 1.

PRINGSHEIM.

'60. Die Coleochætaceen. Jahrb. f. wiss. Bot. **2**, 1.

ROSENBERG.

:01. Ueber die Pollenbildung von Zostera. Med. Stosk. Hogsk. Bot. Inst. 21.

SARGANTS.

'97. The formation of sexual nuclei in Lilium martagon: Spermatogenesis. Ann. of Bot. **11**, 187.

SCHIMPER.

'85. Untersuchungen über die Chlorophyllkörper und die in ihnen homologen Gebilde. Jahrb. f. wiss. Bot. **16**, 3.

SCHNIEWIND-THIES.

:01. Die Reduction der Chromosomenzahl und die ihr folgenden Kerntheilungen in der Embryosackmutterzellen der Angiospermen. Jena.

SHAW.

'98*a*. The fertilization of Onoclea. Ann. of Bot. **12**, 261.

SHAW.

'98*b*. Ueber die Blepharoplasten bei Onoclea und Marsilia. Ber. d. deut. bot. Gesell. **16**, 177.

SMITH.

:00. The achromatic spindle in the spore mother-cell of Osmunda regalis. Bot. Zeit. **30**, 361.

STEVENS, F. L.

'99. The compound oösphere of Albugo bliti. Bot. Gaz. **28**, 149.

STEVENS, F. L.

:01*b*. Gametogenesis and fertilization in Albugo. Bot. Gaz. **32**, 77.

STEVENS, W. C.

'98*a*. Ueber Chromosomtheilung bei der Sporenbildung der Farne. Ber. d. deut. bot. Gesell. **16**, 261.

STEVENS, W. C.

'98*b*. The behavior of kinoplasm and the nucleolus in the division of the pollen mother-cells of Asclepias Cornuti. Kansas Univ. Quart. **7**. 77.

STRASBURGER.

'72. Die Coniferen und die Gnetaceen.

STRASBURGER.

'80. Zellbildung und Zelltheilung. Jena.

STRASBURGER.

'88. Ueber Kern-und Zelltheilung im Pflanzenreich, nebst einem Anhang über Befruchtung. Hist. Beitr. **1**.

STRASBURGER.

'92. Schwarmsporen, Gameten, pflanzlichen Spermatozoiden. Hist. Beitr. 4, **49**.

STRASBURGER.

'95. Karyokinetische Probleme. Jahrb. f. wiss. Bot. **28**, 151.

STRASBURGER.

:00. Ueber Reductionstheilung, Spindelbildung, Centrosomen und Cilienbildner im Pflanzenreich. Hist. Beitr. **6**.

STRASBURGER.

:01. Einige Bemerkungen zu der Pollenbildung bei Asclepias. Ber. d. deut. bot. Gesell. **19**, 450.

THAXTER.

'95*a*. New or peculiar aquatic fungi: Monoblepharis. Bot. Gaz. **20**, 433.

THAXTER.

'95*b*. New or peculiar aquatic fungi: 2, Gonapodya and Myrioblepharis. Bot. Gaz. **20**, 477.

THOM.

'99. The process of fertilization in Aspidium and Adiantum. Trans. Acad. Sci. St. Louis, **9**, 285.

TIMBERLAKE.
:02. Development and structure of the swarmspores of Hydrodictyon. Trans. Wis. Acad. Sci. Arts and Letters **13**, 486.
VAN HOOK.
:00. Notes on the division of the cell and nucleus in liverworts. Bot. Gaz. **30**, 394.
WAGER.
'99. On the eye-spot and flagellum in Euglena viridis. Jour. Linn. Soc. **27**, 463.
WEBBER.
'97*a*. Peculiar structures occurring in the pollen tube of Zamia. Bot. Gaz. **23**, 453.
WEBBER.
'97*b*. The development of the antherozoids of Zamia. Bot. Gaz. **24**, 16.
WEBBER.
97*c*. Notes on the fecundation of Zamia and the pollen tube apparatus of Ginko. Bot. Gaz. **24**, 225.
WEBBER.
:01. Spermatogenesis and fecundation of Zamia. Bu. Plant Ind. U. S. Dept. Agri. Bull. **2**.
WIEGAND.
'99. The development of the microsporangium and microspores in Convallaria and Potomogeton. Bot. Gaz. **28**, 328.
WILLIAMS, CLARA I.
'99. The origin of the karyokinetic spindle in Passiflora cœrulea. Proc. Cal. Acad. Sci. Bot. **1**, 189.
WILSON.
:00. The cell in development and inheritance. New York.
ZACHARIAS.
'87. Beiträge zur Kenntniss des Zellkerns und der Sexualzellen. Bot. Zeit. **45**, 345.
ZIMMERMANN.
'93, '94. Sammel-Referate aus dem Gesammtgebiete der Zellenlehre. Beihf. z. bot. Centb. **3**, 206, 321, 401 (1893), **4**, 81, 161, 321 (1894).
ZIMMERMANN.
'96. Die Morphologie und Physiologie des Pflanzlichen Zellkernes. Jena.

(*To be continued.*)